

BREEDING ROBINS AND NEST PREDATORS: EFFECT OF PREDATOR TYPE AND DEFENSE STRATEGY ON INITIAL VOCALIZATION PATTERNS

BRADLEY M. GOTTFRIED, KATHRYN ANDREWS, AND MICHAELA HAUG

Breeding birds are subject to intense nest-predation pressure by a variety of predators (Gottfried 1978, Gottfried and Thompson 1978). To counteract this pressure, a number of antipredator adaptations have evolved in birds. These adaptations appear to involve nest concealment, distraction displays, and colonial nesting (Skutch 1976). Another antipredator strategy is active nest defense. By imposing the possibility of injury on a predator, a breeding bird may be successful in protecting its nest. Indeed, experimental studies have shown that nesting birds do attack models of nest predators (see Gottfried 1979 and references cited therein). As expected, the intensity of defense increases through the breeding cycle as the amount of parental investment increases (Shields 1984). There is also evidence that birds respond in a different manner to different types of nest predators (Gottfried 1979).

Actual fighting between two animals can be costly in terms of risk of physical injury as well as in time and energy. It has been hypothesized that mechanisms have evolved to reduce the incidence of these interactions (Maynard Smith 1974). As most contests are asymmetric (e.g., the contestants are not equally matched), it is important for each contestant to assess the likelihood that it will win a contest. If, after assessing the situation, a contestant finds that its chances of winning an encounter are low, it may well forgo further interaction, and retreat (Parker 1974). Threat displays may be an important cue in determining the formidability of a particular opponent. Another potential source of information about an opponent may be in its repertoire of vocalizations. Smith (1977) has shown that auditory signals have evolved as an effective way of transmitting information among organisms. Alternative explanations have also been offered (Dawkins and Krebs 1978).

Birds possess a unique repertoire of sounds that are used in territory defense, courtship, and flock maintenance; and a number of studies have shown that birds have the ability to use vocalizations to convey contextual information about motivation levels. Vocalizations conceivably could be used by a nest predator in assessing motivation levels and defense strategy of a breeding bird, or they could be used to signal information about predator-type and form of defense strategy to conspecifics and thus could be used to coordinate nest defense. Predator-induced vocalizations have

been studied extensively in ground squirrels. These organisms give predator-specific types of alarm calls that may also encode information about the predator's activity patterns (Owings and Virginia 1978, Leger et al. 1980, Owings and Leger 1980, Robinson 1980). There have been few similar studies of birds, and most were not experimental (Morton and Shalter 1977, Greig-Smith 1980).

This paper reports on a study in which we examined the vocalizations of American Robins (*Turdus migratorius*) in relation to models of two types of nest predators. We were particularly interested in determining whether initial vocalizations accurately reflected later nest defense strategies (attack or not attack the model), and in the type of predator eliciting the calls.

METHODS AND MATERIALS

The study was conducted from April through July in 1980 and 1981 in old-field habitats in and around St. Paul, Minnesota. We attempted to locate nests soon after egg laying was initiated. Each nest was tested three to five days after the start of incubation. The following technique was used for each test. A stuffed Blue Jay (*Cyanocitta cristata*) or a rubber snake model was affixed to the nest after the female left to feed. After positioning the predator, we retreated to a concealed position approximately 15 m away, from which we could observe subsequent events at the nest. Each test lasted about five min. We used a Uher 4000 Report Monitor tape recorder and a Dan Gibson P650 microphone to record the vocalizations. The tapes were later analyzed with a Kay sonograph model 6061B. In all tests, the vocalizations uttered by the female within five sec of its return to the nest were analyzed. These vocalizations were referred to as the Initial Response Repertoire (IRR). The response of the nesting bird to the predator model was also ranked using the scale presented in Table 1.

RESULTS

Robins primarily used two types of vocalizations in their responses to predator models (Fig. 1): "chirps" and "chucks." "Chirps" were more complex than "chucks," being longer in duration and composed of a wider range of frequencies.

The type of predator model presented influenced the type of vocalization included in a bird's IRR. Eighty-eight percent of the robins tested with the stuffed Blue Jay included "chirps" in their IRR, but only 42% uttered "chirps" in response to the snake ($\chi^2 = 8.62$, $df = 1$, $P < 0.05$). The proportion of robins that included "chucks" in their IRR to the jay was not significantly different from those that included "chucks" to the snake ($\chi^2 = 0.39$, $df = 1$, $P < 0.05$).

"Chirps" were significantly more likely to be included in the IRR of birds that ultimately attacked a model than those that did not attack (92% vs 41%; $\chi^2 = 8.29$, $df = 1$, $P < 0.05$). "Chucks," on the other hand, were more likely to be included in the IRR of robins that did not later attack the predator models (73% vs 38%; $\chi^2 = 4.82$, $df = 1$, $P < 0.05$).

TABLE 1
SCALE USED TO DETERMINE THE AGGRESSION RESPONSE INDEX OF ROBINS

Aggression	Movement pattern
0 = No response	0 = No movement
1 = Approach predator (<5 approaches and retreats/min) no attacks	1 = Little movement (<5 changes in position/min)
2 = Frequent approaches (>5 approaches and retreats/min) no attacks	2 = Medium movement (>5–30 changes in position/min)
3 = Few attacks (<5 strikes on predator/min)	3 = Frenzied movement (>30 changes in position/min)
4 = Frequent attacks (>5 strikes on predator/min)	

Robins that ultimately attacked a jay model were more likely to utter "chirps" than birds that did not attack the jay ($\chi^2 = 5.03$, $df = 1$, $P < 0.05$; Table 2), while "chucks" were more likely to be given by birds that did not later attack the jay models than by those birds that did ($\chi^2 = 3.71$, $df = 1$, $P < 0.05$). Too few robins attacked the snake model to permit a statistical analysis of the data.

To explore the fine details of the "alarm" vocalizations, sonograph tracings were made, and data were collected and subsequently analyzed using 2×2 Analyses of Variance (ANOVA) in an effort to examine possible differences.

The two main effects in the ANOVA were predator type and ultimate form of defense. Three of the seven vocal parameters studied were significantly related to the type of predator model presented (Table 3). Robins uttered twice as many vocalizations/30 sec (particularly "chirps") in response to the jay model as they did to the snake. This was caused by significant differences in the number of "chirps"/30 sec; the number of "chucks"/30 sec was not affected. The increase in the number of vocalizations/30 sec was at the expense of the duration of intervals between notes and not in note length. The ANOVA suggests that the quantitative changes in the IRR in relation to ultimate defense strategy somewhat parallel that of predator type, with birds that later attacked the model uttering significantly more notes in general, and "chirps" in particular, than birds that did not ultimately attack the model.

Robins that ultimately attacked the jay model included a significantly greater number of vocalizations/30 sec in their IRR than those birds that did not attack the model (Table 3). These pre-attack vocalizations con-

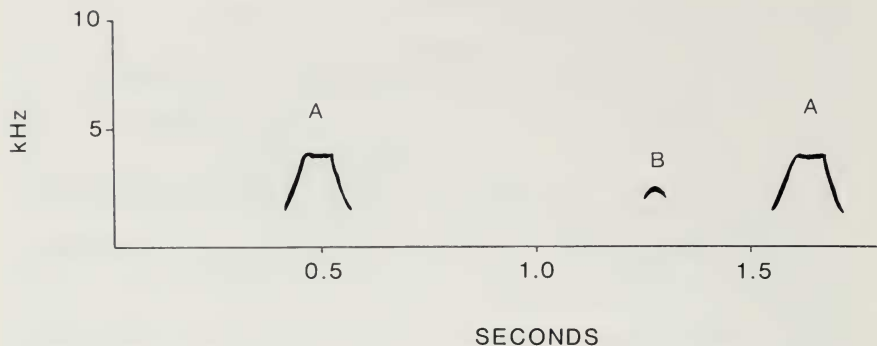


FIG. 1. Sample sonograph tracing of a robin vocalization. Notes with an A are "chirps", those with a B are "chucks."

tained significantly more "chirps" and fewer "chucks" than those robins that did not attack the jay model. Robins that ultimately attacked the jay model also uttered "chucks" whose frequency was significantly different from those birds that did not attack the model.

The IRR of robins that ultimately attacked the snake model contained significantly more notes/30 sec and significantly more "chucks" than the IRR of robins that did not attack the snake. The attacking robins also gave shorter "chirp" vocalizations than robins that did not later attack.

The IRR of robins prior to attacks on the jay and snake models did not contain significantly different numbers of vocalizations/30 sec. This was due to significant but opposite trends in the number of "chirps" and "chucks" (Table 3). Robins that later attacked the jay model uttered an average of 60.3 "chirps"/30 sec, compared to only 20.5/30 sec in those that later attacked the snake. On the other hand, the number of "chucks"/30 sec was 41.8 in the snake experiments and only 1.1 in the jay experiments. Attacks on the jay model were also preceded by "chirps" that contained a shorter time interval between notes than those in the IRR which preceded attacks on the snake model.

The data presented so far indicate that several vocal parameters, particularly the number of vocalizations/30 sec, are related to defense strategy. As the intensity of the responses to the model varied, the data were analyzed with a Spearman Rank Correlation Test to determine if any of the seven vocal parameters was correlated with intensity of nest defense. The intensity of defense was correlated positively with the total number of vocalizations/30 sec ($r_s = 0.76$, $P < 0.05$), the number of "chirps"/30 sec ($r_s = 0.75$, $P < 0.05$), and low ($r_s = 0.57$, $P < 0.05$) and high ($r_s = 0.58$, $P < 0.05$) frequency of "chirps". Duration of "chirps" ($r_s = 0.33$,

TABLE 2
 NUMBER OF AMERICAN ROBINS UTTERING "CHIRPS" AND "CHUCKS" IN RELATION TO
 PREDATOR AND LIKELIHOOD OF ATTACK

Predator model	N	No. giving "chirps" (%)	No. giving "chucks" (%)
Blue Jay			
Attack	22	22 (100)	6 (27)
No attack	10	6 (60)	10 (100)
Total	32	28 (88)	16 (50)
Snake			
Attack	4	2 (50)	4 (100)
No attack	20	8 (40)	6 (30)
Total	24	10 (42)	10 (42)

$P > 0.05$) or their spacing ($r_s = 0.45$, $P > 0.05$) were not correlated with the levels of aggression.

DISCUSSION

Our results suggest that certain parameters, specifically the number of vocalizations a robin utters, the number of major vocalization types ("chirps"), and certain frequency parameters are related to predator type, future defense decisions, and the intensity of future nest defense.

These results are consistent with earlier studies of monkeys and ground squirrels. Vervet Monkeys (*Cercopithecus aethiops*) possess large repertoires of predator-specific alarm calls (Struhsaker 1967, Cheney and Seyfarth 1981). Broadcast of these signals caused free-ranging monkeys to take appropriate defensive measures (Seyfarth et al. 1980). The vocal signals of ground squirrels, although lower in diversity, also show evidence of being predator-specific (Owings and Virginia 1978, Robinson 1980). For example, California Ground Squirrels (*Spermophilus beecheyi*) emit "chatters" and "chats" in the presence of terrestrial predators, and "whistles" when raptors are present. Detailed spectrographic examination of vocalizations was conducted by Owings and Leger (1980) and Leger et al. (1980). "Chatters" evoked by raptors and terrestrial predators were distinct from each other. Owings and Leger (1980) also found the rate of calling to be related to the type of predator. Ground squirrels communicate predator identity through the use of predator-specific vocalization, graded signals, and rates of calling. These data agree with those we collected on robins. Robins were more likely to emit "chirps" than "chucks" in response to the jay model, but were equally likely to utter "chirps" and

TABLE 3
RESULTS OF AN ANOVA OF THE EFFECT OF PREDATOR TYPE AND FUTURE DEFENSE STRATEGY ON VARIOUS VOCALIZATION VARIABLES OF ROBINS

Variable	Main effects					Subeffects								
	Fate		Predator		F	Means		F Values		Snake attack vs no attack				
	Attack \bar{x}	No attack \bar{x}	Blue Jay \bar{x}	Snake \bar{x}		Snake/attack \bar{x}	Snake/no attack \bar{x}	Blue Jay/attack \bar{x}	Blue Jay/no attack \bar{x}		No attack BJ vs snake	Blue Jay attack vs no attack		
Sample size	26	30	32	24		4	20	22	10					
Number of vocalizations/30 seconds	58.6	20.4	19.1 ^a	22.4	6.7 ^a	50.0	13.3	61.4	37.7	1.7	7.9 ^a	7.5 ^a	17.9 ^a	
Number of "chirps"/30 sec	50.3	10.8	24.6 ^a	13.3	11.0 ^a	20.5	10.9	60.3	10.7	28.3 ^a	0.1	43.9 ^a	6.1 ^a	
Number of "chucks"/30 sec	11.3	8.8	2.5	7.8	3.3	41.8	2.3	1.1	24.5	40.9 ^a	12.2 ^a	13.5 ^a	38.6 ^a	
Interval between notes (msec)	205.8	222.2	0.39	188.4	11.4 ^a	285.0	191.4	262.4	182.0	9.4 ^a	7.0 ^a	0.6	0.1	
Duration of "chirps" (msec)	83.7	89.6	2.1	83.8	2.1	82.0	83.9	93.4	83.3	0.3	7.3 ^a	0.1	9.3 ^a	
Low frequency of "chirps" (kHz)	1.4	1.4	0.5	1.4	0.3	1.5	1.4	1.4	1.3	0.6	0.6	0.6	0.6	
High frequency of "chirps" (kHz)	4.4	4.3	3.5	4.4	0.7	4.6	4.5	4.4	4.3	1.0	1.0	4.0 ^a	4.0 ^a	

^a Significant at $P < 0.05$.

"chucks" to the snake. Our study suggests that the ultimate defense strategy (attack or not attack) and intensity of future defense may be encoded in a robin's predator-induced vocalizations. In addition to the quantitative data presented, this idea is supported by qualitative observations at robin nests. In most of the tests where the robins ultimately attacked the predator models, their vocalizations attracted other robins as well as Common Grackles (*Quiscalus quiscula*) and Field Sparrows (*Spizella pusilla*) to the area around the nest. Breeding robins tended to attack these new arrivals, but were usually unable to drive them away. We conducted similar predator-induced vocalization studies with Gray Catbirds (*Dumetella carolinensis*). During these tests, other catbirds were attracted by the vocalizations of the nesting catbird being tested, but unlike robins, these arrivals were tolerated and they may have been involved in attacking the predator models. Robins and catbirds that did not ultimately attack the predator model did not attract other birds to the general area around their nests. By uttering certain numbers and types of vocalizations a bird might be able to gain assistance from other birds in the area in its defense against the predator. Even in our observations of robins where other birds were not involved in defense, the presence of additional agitated birds may be enough to dissuade a predator from continuing its attempt to prey on the contents of the nest.

SUMMARY

The study was conducted to determine if predator-induced vocalizations of breeding American Robins (*Turdus migratorius*) were related to predator identity (Blue Jay [*Cyanocitta cristata*] or snake), later defense strategy (attack or not attack model), and intensity of future defense. Robins used two types of vocalizations in their response to the nest predators: "chirps" and "chucks."

Nesting robins were significantly more likely to utter "chirps" than "chucks" in tests with a stuffed Blue Jay. All birds that later attacked the jay included "chirps" in their repertoire; all those that did not attack included "chucks" in their repertoire. In experiments with a snake model, both types of vocalizations were equally likely to be given. The number of vocalizations/30 sec and the number of "chirps"/30 sec were consistently related to predator type, future defense strategy, and intensity of future defense.

ACKNOWLEDGMENTS

We wish to thank R. Christman and C. and D. Fiedler for their assistance and encouragement. Two referees, D. Shedd and W. M. Shields provided valuable suggestions. F. Vukmonich provided vital electronics assistance. The study was funded by National Science Foundation Grant CDP-8010620, and by a National Science Foundation Undergraduate Research Participation Grant.

LITERATURE CITED

- CHENEY, D. AND R. SEYFARTH. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour* 76:25-61.

- DAWKINS, R. AND J. R. KREBS. 1978. Animal signals: information or manipulation? Pp. 282-309 in *Behavioural ecology* (J. R. Krebs and N. B. Davies, eds.). Sinauer Associates, Sunderland, Massachusetts.
- GOTTFRIED, B. 1978. An experimental analysis of the interrelationship between nest density and predation in old-field habitats. *Wilson Bull.* 90:643-646.
- . 1979. Anti-predator aggression in birds nesting in old-field habitats: an experimental analysis. *Condor* 81:251-257.
- AND C. THOMPSON. 1978. Experimental analysis of nest predation in an old-field habitat. *Auk* 95:304-312.
- GREIG-SMITH, P. 1980. Parental investment in nest defense by Stonechats (*Saxicola torquata*). *Anim. Behav.* 28:604-619.
- LEGER, D., D. OWINGS, AND D. GELFAND. 1980. Single-note vocalizations of California Ground Squirrels: graded signals and situation-specificity of predator and socially evoked calls. *Z. Tierpsychol.* 52:227-246.
- MAYNARD SMITH, J. 1974. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47:209-222.
- MORTON, E. AND M. SHALTER. 1977. Vocal responses to predators in pair-bonded Carolina Wrens. *Condor* 79:222-227.
- OWINGS, D. AND R. VIRGINIA. 1978. Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Z. Tierpsychol.* 46:58-70.
- AND D. LEGER. 1980. Chatter vocalizations of California ground squirrels: Predator- and social-role specificity. *Z. Tierpsychol.* 54:163-184.
- PARKER, G. 1974. Assessment strategy and the evolution of fighting behavior. *J. Theor. Biol.* 65:571-578.
- ROBINSON, S. 1980. Antipredator behaviour and predator recognition in Belding's Ground Squirrels. *Anim. Behav.* 28:840-852.
- SEYFARTH, R., D. CHENEY, AND P. MARLER. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210:801-803.
- SHIELDS, W. M. 1984. Barn Swallow mobbing: self-defense, collateral kin defense, group defense, or parental care? *Anim. Behav.* 32:132-148.
- SKUTCH, A. F. 1976. *Parent birds and their young*. Univ. Texas Press, Austin, Texas.
- SMITH, W. 1977. *The behaviour of communicating: a theoretical approach*. Harvard Univ. Press, Cambridge, Massachusetts.
- STRUHSAKER, T. 1967. Auditory communication among vervet monkeys (*Cercopithecus aethiopus*). Pp. 281-324 in *Social communication among primates* (S. Altmann, ed.), Univ. Chicago Press, Chicago, Illinois.

DEPT. BIOLOGY, COLL. ST. CATHERINE, ST. PAUL, MINNESOTA 55105. (PRESENT ADDRESS BMG: DEPT. BIOLOGY, ARMSTRONG STATE COLLEGE, SAVANNAH, GEORGIA 31419.) ACCEPTED 5 JAN. 1985.